RESOURCE PARTITIONING BY CARIBBEAN CORAL REEF SPONGES: IS THERE ENOUGH FOOD FOR EVERYONE ?

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Sponges are known to graze primarily on the ultraplankton fraction (plankton < 5µm) of the water column community and have been implicated as primary coral reef consumers of ultraplankton, but it is unknown if there is inter- or intraspecies competition for food resources. I characterised diet and retention efficiency of three co-occuring species of sponge at Chub Cay Reef, Bahamas (25°22'82"N, 77°51'93"W). The erect tube sponge *Callyspongia vaginalis*, the mounding sponge *Spongia tubulifera*, and small *Aplysina fistularis* were conspicuous and common members of the benthic community, and had mean heights above the substrate of 22.5, 7.0, and 1.2cm, respectively. Ambient and exhalent current water samples were collected by snorkelers and analyzed for ultraplankton using flow cytometry. *Callyspongia vaginalis* retained only *Synechococcus*-type cyanobacteria with an efficiency of 90%. In contrast, the diets of *S. tubulifera* and *A. fistularis* were more reflective of the overall water column community consisting of heterotrophic bacteria, *Prochlorococcus*, *Synechococcus*-type cyanobacteria and autotrophic picoeucaryotes. *Spongia tubulifera* had retention efficiencies of 41, 29, and 86% for heterotrophic bacteria, *Prochlorococcus*, and *Synechococcus*-type cyanobacteria, respectively. Retention efficiencies were highest for *A. fistularis*, the smallest sponge, with 96% for heterotrophic bacteria, 95% for *Prochlorococcus*, 99% for *Synechococcus*-type cyanobacteria and 100% for autotrophic picoeucaryotes. Food availability increased closer to the benthos such that an order of magnitude more ultraplankton cells were available to *S. tubulifera* and *A. fistularis*. Overall low abundance of food particles ($<10^5$ cells ml^{-1}) 22cm above the benthos may prevent effective capture by choanocytes. Competition for food resources between phylla is most likely the cause of the resource partitioning found at this location rather than competition between sponges. ❒ *Porifera, feeding, ultraplankton, Caribbean, coral reef, competition.*

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Given that oligotrophic conditions inherently characterise coral reefs, it is not surprising that they are net sinks for all types of planktonic foods, such as zooplankton (Glynn, 1973), nanoplankton (Glynn, 1973), and picoplankton (Buss & Jackson, 1981; Ayukai, 1995; Charpy & Blanchot, 1998), consumed by sessile benthic organisms. However, difficulties in measuring food availability at a scale relevant to these organisms themselves has restricted our understanding of the role of competition for food by benthic suspension feeders. This primarily has been limited by large sample sizes required to quantify naturally occurring, low densities of many food types. Ultraplankton (plankton < 5µm; Murphy & Haugen, 1985) is the most abundant food source on coral reefs both numerically and in terms of total carbon (Ayukai, 1992, 1995; Pile, 1997; Charpy & Blanchot, 1998), and has recently been found to be the major component of the diet of sponges (Reiswig, 1971; Pile, 1997), ascidians (Pile & Young, in review), and soft corals (Fabricius et al., 1995a, b; Ribes et al., 1998) common to coral reefs. Considering that the potential guild of active and passive suspension feeders that will graze on ultraplankton is quite large it is reasonable to suspect that competition for food resources could limit the distribution of some organisms.

Sponges are known to graze primarily on the ultraplankton fraction of the water column community (Pile et al., 1996, 1997; Pile, 1997), and have been implicated as the primary coral reef consumers of ultraplankton (Reiswig, 1971; Pile, 1997; Charpy & Blanchot, 1998) . On Pacific reefs, 90% of the ultraplankton is removed from water that passes over a reef and it

TABLE 1. Mean ultraplankton availability (10^3 cells ml^{-1} ± sd, n=10) at Chub Cay, Bahamas.

Type of ultraplankton	Mean height above bottom (cm)		
	22	7	1.4
Procaryotes			
Heterotrophic bacteria	4.99 (1.37)	77.1 (48.9)	116.0 (49.2)
Prochlorococcus	2.00 (0.44)	45.8 (26.6)	37.2 (17.9)
Synechococcus-type cyanobacteria	8.59 (12.2)	93.8 (81.9)	177.0 (15.3)
Eucaryotes			
Autotrophic eucaryotes (<3μm)	0.10 (0.11)	16.2 (9.37)	63.9 (48.3)

has been suggested that this is the result of grazing by the benthos (Ayukai, 1995). In the Caribbean, sponges are the dominant benthic invertebrate, contributing up to 2.5kgm^2 of the benthic biomass (Wilkinson, 1987). Coneurrent with this high biomass the sponge eommunity is very diverse with morphologies ranging from encrusting to massive (Wilkinson, 1987). High abundanee and species diversity of sponges eoupled with oligotrophic conditions eommon to coral reefs could require partitioning of food resourees between sponges or with other members of the guild of primary eonsumers of ultraplankton whieh is not found in more eutrophic ecosystems (Stuart & Klumpp, 1984; Lesser et al., 1992).

Abelson et al. (1993) hypothesised that the morphology of eoral reef organisms modifies the flow patterns around them such that it predisposes their diets. In their model, organisms with a high slenderness ratio (the ratio between body height and downmost width > 1) will graze on fine particulate matter whereas organisms with a low slenderness ratio (< 1) will feed primarily on bed load partieles. Upright tubular sponges, gorgonians and other soft eorals all have high slenderness ratios and it is highly likely that they will utilise the same food resourees. Small mounding, massive, and enerusting sponges all have low slenderness ratios and would be able to exploit an unoeeupied niehe by grazing on ultraplankton if all other low slenderness ratio organisms (i.e. flattened types of eorals, solitary fungiid coral species, and bryozans) grazed primarily on bed load particles. Therefore, in this study I quantified the food availability and diet of three co-oceuring speeies of demosponges on a coral reef with varying slenderness ratios to determine if there was greater competition for food resourees for speeies with high slenderness ratios.

MATERIALS AND METHODS

Diets and retention efficiencies were measured for three co-oeeuring species of sponge at Chub Cay Reef, Bahamas (25°22'82"N, 77°51'93"W). Chub Cay Reef is a patch reef that has a maximum depth of 5m. The ereet tube sponge *Callyspongia vaginalis*, the mounding sponge *Spongia tubulifera*, and very small *Aplysina fistularis* were conspicuous and common members of the benthie eommunity and had mean heights (n=10) above the substrate of 22.5 (± 3.8 sd), 7.0 (± 1.3 sd), and 1.2 (± 0.4 sd)cm respectively.

Retention of ultraplankton was quantified from 1ml water samples collected using 5cc syringes from 10 individuals of each speeies while snorkeling to a depth of no greater than 3m. Samples were taken from water adjaeent to the sponge and from the exhalent eurrent of each individual and preserved for flow eytometry using standard protoeols (Campbell et al., 1994). Ultraplankton populations were quantified using an Epie Elite flow eytometer (Coulter Eleetronics Corporation, Hialeah, Florida) at Harbor Braneh Oceanographie Institution, following the techniques of Marie et al. (1996). Orange fluorescence (from phyeoerythrin), red fluoreseenee (from ehlorophyll), and green fluorescenee (from DNA stained with SYBR Green) were eolleeted through band pass interferenee filters at 575, 680, and 450nm, respeetively. The five measured parameters (forward- and right-angle light scatter (FALS and RALS), orange, red, and green fluorescenee) were recorded on 3-decade logarithmie seales, sorted in list mode, and analyzed with a eustom-designed software (CYTOWIN; Vaulot, 1989). Ultraplankton populations were identified to general eell types of heterotrophie bacteria (HBac), *Prochlorococcus* (Pro), *Synechococcus*-type cyanobaeteria (Syn), and autotrophic eucaryotes <3μm (Peuc), visually confirmed (except for *Prochlorococcus*), and mean eell diameter measured (n=50) using epifluorescenee mieroseopy.

Differences between cell counts from ambient and exhalent eurrent water of eaeh type of ultraplankton were analyzed using two tailed t-tests for each spceies of sponge with a Bonferroni-transformed experimentwise ; of 0.00625 to determine the effects of sponges on

TABLE 2. Mean 10^3 cells ml^{-1} (± sd, n=10) in the exhalent current demonstrating the effect of each sponge on the four types of ultraplankton. Individual t-tests comparing mean cell concentrations to ambient cell concentrations (Table 1). * p < 0.00625.

Species of Sponge	Height (cm)	Heterotrophic bacteria	*Prochlorococcus*	*Synechococcus*-type cyanobacteria	Autotrophic picoeucaryotes
Callyspongia vaginalis	22.5	5.08 (0.96)	2.12 (0.58)	0.90* (0.23)	0.04 (0.05)
Spongia tubulifera	7.0	45.8 (0.49)	32.3 (0.49)	13.5* (0.29)	9.09 (0.21)
Aplysina fistularis	1.2	4.2* (0.42)	1.70* (0.24)	2.03* (1.43)	0.17* (0.06)

ultraplankton (Zar, 1984). The mean retention efficiency for each sponge was calculated as ((mean cell count ambient - mean cell count exhalent)/mean cell count ambient)x100 for each type of ultraplankton. Student t tests, one tailed, were used to determine if the retention efficiency for each type of ultraplankton was significantly >0 employing a Bonferronni transformed experimentwise error of ∝=0.0001, p=0.00625.

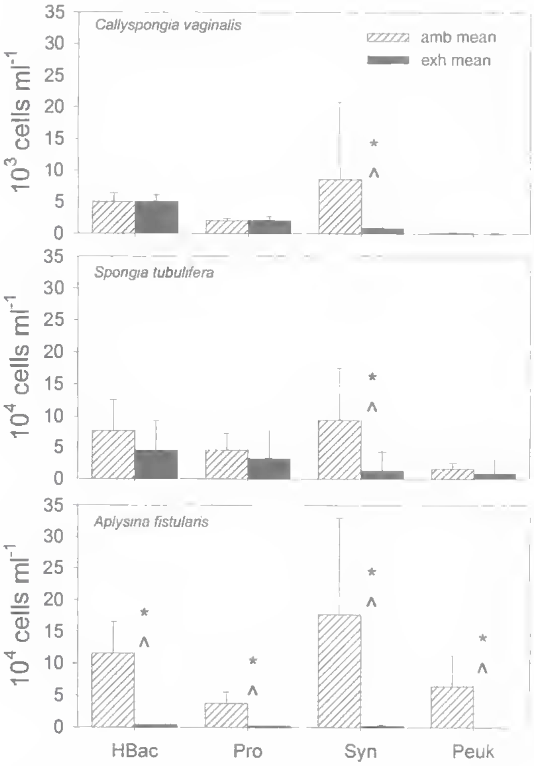

FIG. 1. Effect of each sponge on ultraplankton populations. Concentration of each type of ultraplankton in ambient water and water from the exhalent currents of each sponge. Stippled bars are for ambient water and black bars for water from the exhalent current. Abbreviations: Hbac= heterotrophic bacteria, Syn= Synechococcus-type cyanobacteria, and Peuk= autotrophic eukaryotes <3µm. Note that the y axis is an order of magnitude less for *C. vaginalis*. * Cell concentrations between ambient water and exhalent current water which are significantly different (paired t-test with a Bonferroni transformed experimentalwise ∝<0.00625).

RESULTS

Ultraplankton abundance decreased with height above the benthos (Table 1). Abundance at all three heights followed the pattern of *Synechococcus*-type cyanobacteria as the most abundant cell type followed by heterotrophic bacteria, *Prochlorococcus*, and autotrophic eucaryotes < 3µm were the least abundant. Ultraplankton abundance increased from $1.57x10^4$ cells ml^{-1} at 22cm to $29.1x10^4$ cells ml^{-1} at 1.4cm from the benthos.

Callyspongia vaginalis retained only *Synechococcus*-type cyanobacteria (Table 2, Fig. 1) with an efficiency of 90% (Fig. 2). In contrast, the diets of *S. tubulifera* and *A. fistularis* were more reflective of the overall water column community consisting of heterotrophic bacteria, *Prochlorococcus*, *Synechococcus*-type cyanobacteria and autotrophic picoeucaryotes (Table 2, Fig. 1). *Spongia tubulifera* had retention efficiencies of 41, 29, and 86% for heterotrophic bacteria, *Prochlorococcus*, and *Synechococcus*-type cyanobacteria respectively (Fig. 2). Retention efficiencies were highest for *A. fistularis*, the smallest sponge, with 96% for heterotrophic bacteria, 95% for *Prochlorococcus*, 99% for *Synechococcus*-type cyanobacteria and 100% for autotrophic picoeucaryotes (Fig. 2).

DISCUSSION

Typical of other demosponges all three species grazed primarily on the ultraplankton fraction of the water column community (Reiswig, 1971; Pile et al., 1996, 1997; Pile, 1997). Retention efficiencies by *C. vaginalis* and *S. tubulifera* were substantially lower than those previously reported for demosponges and this may be related

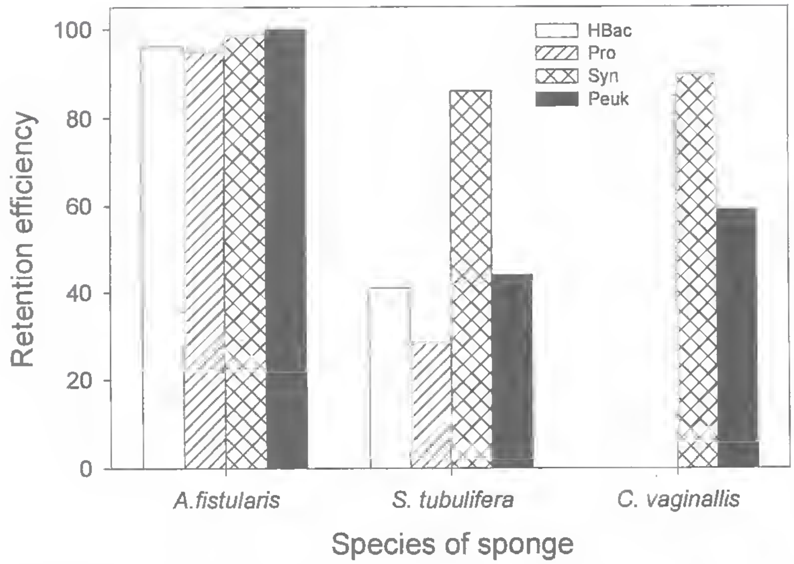

FIG. 2. Retention efficiency (x ± sd, n = 10) for each species of sponge for each type of ultraplankton. Abbreviations: Hbac = heterotrophic bacteria, Syn = *Synechococcus*-type cyanobacteria, and Peuk = autotrophic eukaryotes <3μm

to the low abundance of cells available to the sponges (Reiswig, 1971; Pile et al., 1996, 1997; Pile, 1997). When the abundance of ultraplankton approached those normally found on coral reefs (Ayukai, 1995; Pile, 1997), such as those in water surrounding *A. fistularis*, retention efficiencies are similar to those previously observed (Reiswig, 1971; Pile, 1997). It should be noted that at Chub Cay Reef *Synechococcus*-type cyanobacteria was the most abundant food source, which is unusual in that bacteria are normally the most abundant food source on coral reefs (Ayukai, 1995; Pile, 1997).

Increasing ultraplankton availability nearer to the benthos opposes the pattern of ultraplankton community structure in shallow waters found in the Red Sea (Yahel et al., 1998) and Lake Baikal (Pile et al., 1997) where abundance decreases closer to the benthos. As predicted by the model of Abelson et al. (1993) ultraplankton availability increased closer to the benthos and this trend is most likely due to decreasing competition for it as a food source. Ultraplankton abundance was extremely low (< 10^5 cells ml^{-1}) 22cm above the bottom and availability increased closer to the benthos such that an order of magnitude more ultraplankton cells were available to *S. tubulifera* and *A. fistularis*. Overall low abundance of food particles 22cm above the benthos may be preventing effective capture by the choanocytes and merits further investigation.

Competition between phylla for food resources is most likely the cause of the resource partitioning found at this reef rather than competition between sponges. The other major benthic organisms at Chub Cay Reef are gorgonian corals *Gorgonia flabellum*, *G. ventalina*, *Plexaura flexuosa*, and *P. porosa*. Recently, soft corals have been found to significantly impact ultraplankton communities. In the Caribbean *Plexaura flexuosa* and *P. porosa* graze on the ultraplankton fraction >3μm (Ribes et al., 1998) while in the Red Sea the soft corals *Dendronephthya hemprichi*, *D. sinaiensis*, and *Scleronephthya corymbosa* and the gorgonian *Acabaria sp.* have been found to graze on plankton down to *Synechococcus*-type cyanobacteria (typically 1.2-1.8μm) (Fabricius et al., 1995b). Soft coral biomass is considerable in some communities were sponges are also prolific (Kinzie, 1973) and may be a significant competitor for ultraplankton. Since soft corals and gorgonians typically have a higher s/r ratio they will most likely impact a zone of water that is higher from the benthos than sponges with a low s/r ratio. Most other organisms with low s/r ratios, such as hard corals, bryozans, and bivalves are typically bed load feeders (e.g. Abelson et al., 1993; Jørgensen, 1996; Riisgård & Manriquez, 1997). Sponges with a low s/r ratio may be the only group of organisms to graze on ultraplankton. If this is true, then they have cornered a niche which has allowed for their success in benthic communities.

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